A Reexamination of the Relationship between Electrofishing Catch Rate and Age-0 Walleye Density in Northern Wisconsin Lakes

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Abstract.—We quantified the relationship between the population density (number/acre) of age-0 walleyes *Sander vitreus* (formerly *Stizostedion vitreum*) and electrofishing catch per effort (CPE; number/mi) in 19 Wisconsin lakes to update a 1982 analysis by Serns, who used linear regression through the origin to develop a model from a small data set that has been widely used to estimate age-0 walleye density from electrofishing CPE. We added new data, explicitly tested for the linearity of the relationship, and accounted for the effect of measurement errors. We found that electrofishing CPE was nonlinearly related to the population density of age-0 walleyes, which indicated that the catchability of age-0 walleyes to electrofishing declined with population density. The measurement errors in electrofishing CPE were more than nine times as great as those in age-0 walleye population density, so that the parameters of the relationship between electrofishing CPE and age-0 walleye density were accurately estimated by ordinary-least-squares linear regression. Among lakes, the variation in the catchability of age-0 walleyes to electrofishing was positively related to the variation in specific conductivity but not to the variation in other physical features (shoreline complexity or littoral area) or chemical features (alkalinity or pH). Within lakes, the variation in the catchability of age-0 walleyes to electrofishing was negatively related to the variation in temperature at the time of sampling. We recommend that electrofishing CPE only be used as a crude index of age-0 walleye population density.

Fishery surveys often assume that gear efficiency does not change with density of the target species. Thus, the portion of a fish population that is removed by a single unit of fishing effort, defined as the catchability coefficient *q*, is often assumed to be constant in the equation

$$\frac{C}{f} = q \times \frac{N}{A},$$

where *C* is catch, *f* is fishing effort, *N* is the number of fish, and *A* is the area occupied by the fish stock (Ricker 1975; Richards and Schnute 1986; Gulland 1988; Hilborn and Walters 1992; Quinn and Deriso 1999). The catch equation assumes that catch per effort (CPE; *C/f*) is linearly related to density (*N/A*) with a slope equal to *q* (Peterman and Steer 1981). However, catchability may vary inversely

with fish density if searching is not random or if handling time is long (Paloheimo and Dickie 1964; Peterman and Steer 1981; Arreguin-Sanchez 1996; Shuter et al. 1998). If *q* varies inversely with fish density, the fraction of the population caught by each unit of fishing effort increases as fish abundance decreases, thereby causing fish density to be overestimated (Shardlow et al. 1985) and overfishing to go undetected (Hilborn and Walters 1992). In addition, testing for the nonlinearity of catchability is difficult because fish density is usually estimated with error, which biases estimates from ordinary-least-squares regression of CPE against density (Ricker 1975; Fuller 1987; Quinn and Deriso 1999). Lastly, the relationship between CPE and density is often noisy because many factors cause *q* to vary (Hilborn and Walters 1992).

Electrofishing is often used as a fish sampling method, and therefore theCPE of the gear is often used to index density of a target species (Serns 1982, 1983; Hall 1986; McInerny and Degan 1993;

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McInerny and Cross 2000). Serns (1982) previously quantified the relationship between mark–recapture estimates of the density (number/acre) of age-0 walleyes *Sander vitreus* (formerly *Stizostedion vitreum*) and electrofishing CPE (number/mi) in 13 northern Wisconsin lakes. He found that electrofishing CPE explained most of the variation in age-0 walleye density estimated by mark–recapture ($r^2 = 0.96$) and suggested that electrofishing CPE could therefore be used to reliably estimate the population density of age-0 walleyes (Serns 1982). Serns (1982) used linear regression through the origin to describe the relationship between density and electrofishing CPE, which explicitly assumes that the relationship is linear and that measurement errors in electrofishing CPE are negligible in relation to measurement errors in population density. He did not test for the linearity of the relationship between age-0 walleye density and electrofishing CPE, nor did he account for measurement errors in electrofishing CPE when estimating model parameters (Serns 1982).

Our objective was to determine the most appropriate model (linear or nonlinear) of the relationship between electrofishing CPE and age-0 walleye density after accounting for measurement errors. To meet our objective, we first increased the power of our analysis by adding data that were collected since Serns' (1982) analysis. Next, we used Monte Carlo methods and an errors-in-variables model to account for measurement errors in electrofishing CPE and age-0 walleye population density and then tested the linearity of the relationship between the two variables. Last, we compared our bias-corrected model with Serns' (1982) model to determine whether electrofishing CPE could be used to reliably estimate age-0 walleye population density in northern Wisconsin lakes.

Methods

Study lakes.—We used mark–recapture estimates of age-0 walleye abundance from 19 lakes in northern Wisconsin (Figure 1). The physical characteristics of the lakes varied widely: surface area ranged from 67 to 3,054 acres, shoreline length ranged from 1.2 to 19.7 mi, shoreline development factor (SDF), determined from the equation

$$\left(\text{SDF} = \frac{\text{Miles}}{2\sqrt{\pi(\text{Acres}/640)}} \right)$$

ranged from 1.05 to 2.96, and littoral area (% of surface area covering depths ≤ 20 ft) ranged from 20% to 100% (Table 1). The chemical charac-

FIGURE 1.—Map showing the locations of 19 Wisconsin lakes in which electrofishing catch rate (number/mi) and age-0 walleye population density (number/acre) were estimated during 1958–1999.

teristics of the lakes also varied widely: alkalinity ranged from 11 to 110 ppm, specific conductivity at 25°C (77°F) ranged from 24 to 221 μS/cm, and pH ranged from 6.4 to 8.6 (Table 1).

Field sampling.—Age-0 walleyes were sampled in autumn (mid-September to mid-October) of 1958–1999 by use of 230-V AC electrofishing boats equipped with transformers. The boats were of standard design and utilized two booms, each fitted with three flexible, corrosion-resistant, steel-tube dropper electrodes. For both mark and recapture samples, the entire shoreline, including islands, was sampled at a speed of 1.4–1.6 mi/h, with no unavoidable stops or resampling of shoreline. Boats were run as close to shore as the engine draft allowed, so sampling depth was within the range of 1–4 ft. Crews included two netters and one operator, except on Escanaba Lake during 1975–1978, when only one netter was used (Serns 1982). Additional personnel, when available, were used to process catches on a continuous basis; otherwise, catches were processed at the end of the sampling run. The operator was responsible for maintaining the boat speed and power settings that elicited uniform taxis and narcosis without inducing postcapture mortality, which required operator judgment and communication with netters. Boat speed is an important factor in electrofishing efficiency because too much speed causes targets to

TABLE 1.—Physical and chemical characteristics of 19 northern Wisconsin lakes in which mark–recapture surveys of age-0 walleye abundance were completed during 1958–1999. The acronym SDF stands for shoreline development factor, which is defined as miles/(2[π\{acres/640\}$^{1/2}$]).

Lake	County	Surface area (acres)	Shoreline (mi)	SDF	Littoral area (%)	Alkalinity (ppm)	Specific conductivity (μS/cm)	pH
Arrowhead	Vilas	99	1.9	1.36	40	38	99	6.8
Bearskin	Oneida	384	5.9	2.15	92	48	102	6.9
Big Arbor Vitae	Vilas	1,090	10.7	2.31	80	51	117	7.6
Big Crooked	Vilas	682	5.0	1.37	65	14	39	7.2
Big McKenzie	Burnett	1,185	7.1	1.47	55	84	142	8.6
Big St. Germain	Vilas	1,617	6.4	1.14	80	37	83	8.2
Bullhead	Manitowoc	67	1.2	1.05	20	110	221	8.3
Butternut	Forest	1,292	7.8	1.55	75	45	101	7.4
Escanaba	Vilas	293	5.1	2.13	60	23	50	7.4
Lost Canoe	Vilas	249	4.0	1.81	40	21	51	8.3
Plum[a]	Vilas	220	3.3	1.59	81	31	50	7.6
Plum[b]	Vilas	1,108	13.8	2.96	55	50	90	7.2
Round	Sawyer	3,054	19.7	2.54	20	21	53	6.4
Shell	Washburn	2,576	10.2	1.43	36	11	24	7.0
Sherman	Vilas	123	2.2	1.42	100	13	30	6.8
Siskiwit	Bayfield	330	4.1	1.61	100	15	61	6.2
Sparkling	Vilas	127	2.3	1.46	40	42	92	7.4
Star	Vilas	1,206	11.0	2.26	20	32	63	8.0
Wolf	Vilas	393	4.4	1.58	65	65	178	8.2

[a] Located on the Wisconsin–Michigan border, with about 90% of its surface area in Gogebic County, Michigan.
[b] Located entirely in Vilas County, Wisconsin.

be overrun and too little speed allows fish to escape the electric field. We found that the window for efficient boat speed was between 1.4 and 1.7 mi/h, which is not difficult to attain with a veteran crew. We therefore used veteran crews throughout the collection of data for this study to ensure greater efficiency. Age-0 walleyes were measured for total length ($N = 100$), marked by removal of a fin, and released. Churchill (1963) found that fin removal did not reduce survival of age-0 walleyes, so we deduced that fin removal would not bias mark–recapture estimates. Age-0 walleyes were separated from age-1 walleyes by length frequency analysis after verification with scale analysis. The number of age-0 walleyes captured per mile of shoreline was used to characterize electrofishing CPE.

To estimate population density, electrofishing was continued on one subsequent night in Big St. Germain, Bullhead, Butternut, Gilmore, Pike, Round, and Shell lakes, and on 3–5 subsequent nights in all other lakes. The abundance of age-0 walleyes was estimated with Bailey's modification of the Peterson estimator for lakes sampled only once for marking and once for recapturing and with the Schnabel estimator for lakes sampled on 3–5 nights (Ricker 1975). We used electrofishing for both marking and recapturing age-0 walleyes because the fish congregate inshore during autumn and are therefore fully vulnerable to capture by

electrofishing (Serns 1982). We sampled the entire shoreline to ensure that marked and unmarked fish were fully vulnerable to capture. Confidence intervals for all estimates were based on 95% confidence intervals (CIs) from the Poisson distribution for the number of recaptures (Ricker 1975). Standard deviations of the estimates were estimated using variance approximations presented by Ricker (1975). We excluded estimates for which the coefficient of variation was larger than 0.40 because we judged such estimates to be of unacceptably low precision (Beard et al. 1997; Hansen et al. 2000; Rogers et al. 2003). We also excluded estimates for which the standard deviation could not be determined because we could not simulate measurement errors for such estimates (see below).

Statistical analysis.—To determine whether the catchability of age-0 walleyes by electrofishing varied with density, we modeled electrofishing CPE as a nonlinear function of age-0 walleye density:

$$\frac{C}{f} = \alpha \left(\frac{N}{A}\right)^{\beta+1}, \qquad (1)$$

where β expresses the degree of curvature in the relationship between CPE and density and α provides an estimate of q near the origin (Peterman and Steer 1981). Because CPE (C/f) and density (N/A) were distributed lognormally, we estimated parameters from the transformed model

$$\log_e\left(\frac{C}{f}\right) = b_0 + b_1 \log_e\left(\frac{N}{A}\right), \qquad (2)$$

where the intercept $b_0 = \log_e \alpha$ and the slope $b_1 = \beta + 1$. We estimated the slope using ordinary least squares as the basis for estimating a bias-corrected slope and 95% confidence limits using Monte Carlo methods. For comparison, we estimated the geometric mean (GM) functional regression line, which is often used when the x-variable is measured with error but which assumes that the measurement errors in the dependent and independent variables are of similar magnitude (Ricker 1975; Sokal and Rohlf 1981).

The parameters in the $\log_e$ transformed model may be biased (the slope too low and the intercept too high) when estimated by ordinary least squares because of errors in the estimates of N (Peterman and Steer 1981; Shardlow et al. 1985). We therefore used Monte Carlo simulations to estimate a bias-corrected slope and intercept for the relationship between $\log_e$ transformed CPE and $\log_e$ transformed density from observed measurement errors in N. One thousand normally distributed random values of density were generated for each lake based on the estimated density and standard deviation of each estimate. Lakes with negative simulated density values were omitted because they had highly variable density estimates. Each random value of density was regressed against the electrofishing CPE by ordinary least squares (linear regression) to estimate a set of 1,000 biased slopes and intercepts. The set of 1,000 biased slopes and intercepts were then used to estimate a corresponding set of 1,000 bias-corrected slopes and intercepts as follows:

$$b_{bc} = b_{ols} + (b_{ols} - b_{mc}), \qquad (3)$$

where the b_{bc} are the 1,000 bias-corrected slopes or intercepts, b_{ols} is the single slope or intercept estimated by linear regression for the original data, and the b_{mc} are the 1,000 biased slopes or intercepts estimated by Monte Carlo simulations. To test for density dependence in catchability, the bias-corrected slope was tested for a significant difference from 1.0 using the upper and lower 0.025 percentiles of the distribution of bias-corrected slopes (simulated 95% CI). We concluded that the relationship was linear if the simulated 95% CI of the slope included 1.0 and nonlinear if the simulated 95% CI of the slope did not include 1.0.

To estimate the measurement error ratio between electrofishing catch-rate and age-0 walleye density, we substituted our estimate of the bias-corrected slope into an errors-in-variables model with known variance:

$$\beta_1^2 m_{xy} - \beta_1(m_{yy} - \delta m_{xx}) - \delta m_{xy} = 0, \qquad (4)$$

where β_1 is the bias-corrected slope, m_{yy} is the variance in y, m_{xx} is the variance in x, m_{xy} is the covariance between x and y, and δ is the y/x measurement error ratio that is solved iteratively (Fuller 1987; Quinn and Deriso 1999). We used the inverse of the measurement error ratio to estimate the slope of the relationship between age-0 walleye population density (as the dependent variable) and electrofishing catch rate (as the independent variable), which was the form of the relationship originally developed by Serns (1982). We then compared our bias-corrected model to the model estimated by Serns (1982) as a way of judging the effect of measurement errors on the model that has been widely used to estimate age-0 walleye population density.

To test the influence of data from Escanaba Lake, which equaled as many observations as from all other lakes combined, we compared the slopes (b_1) and intercepts (b_0) of the linear relationships between electrofishing CPE ($\log_e[C/f]$) and age-0 walleye density ($\log_e[N/A]$) between Escanaba Lake and the other lakes. We tested the degree of curvature in the relationships between Escanaba Lake and other lakes using the interaction between age-0 walleye density and lake group (Escanaba Lake versus the others). If the interaction term was not significant, we concluded that relationships between electrofishing CPE and density were of similar shape in Escanaba Lake and the other lakes. We tested the similarity of the catchability of age-0 walleyes to electrofishing between Escanaba Lake and other lakes using the main effect for lake groups (Escanaba Lake versus other lakes). If the main effect was not significant, we concluded that catchability was similar in Escanaba Lake and the other lakes.

To determine whether catchability was affected by factors among and within lakes, we assessed whether physical and chemical factors described significant residual variation in the relationship between electrofishing catch rate and age-0 walleye density via the equation

$$\frac{C}{f} = \alpha\left(\frac{N}{A}\right)^{\beta+1} X_1^{b_2} \cdots X_n^{b_n}, \qquad (5)$$

where the X variables are external factors that explained any variation in the electrofishing catch

TABLE 2.—Number of mark–recapture estimates of age-0 walleye abundance in northern Wisconsin lakes during 1958–1999 (old = analyzed by Serns 1982; new = this study; the terms "excluded" and "included" refer to exclusion from and inclusion in the present analysis).

Lake	County	Acres	Excluded			Included		
			New	Old	Total	New	Old	Total
Arrowhead	Vilas	99					1	1
Bass-Patterson	Washburn	188	1		1			
Bearskin	Oneida	384					2	2
Big Arbor Vitae	Vilas	1,090				1		1
Big Crooked	Vilas	682	1	1	2	6		6
Big McKenzie	Burnett	1,185				1		1
Big St. Germain	Vilas	1,617		1	1	1	1	2
Bullhead	Manitowoc	67					1	1
Butternut	Price	1,006		1	1			
Butternut	Forest	1,292				2		2
Escanaba	Vilas	293				36	3	39
Gilmore	Oneida	301		1	1			
Johnson	Vilas	78		1	1			
Lost Canoe	Vilas	249				3		3
Pike	Price	806		1	1			
Pike-Round	Price	1,532		1	1			
Plum[a]	Vilas	220	3		3	3		3
Plum[b]	Vilas	1,108				1		1
Round	Price	726		1	1			
Round	Sawyer	3,054				1		1
Shell	Washburn	2,576					1	1
Sherman	Vilas	123	1		1	1		1
Siskiwit	Bayfield	330	1		1	1		1
Sparkling	Vilas	127					4	4
Squaw	Vilas	785	1		1			
Star	Vilas	1,206				1		1
Wolf	Vilas	393	1		1	6		6
Total			9	8	17	64	13	77

[a] Located on the Wisconsin–Michigan border, with about 90% of its surface area in Gogebic County, Michigan.

[b] Located entirely in Vilas County, Wisconsin.

rate that was not explained by age-0 density. To explain the variability in catchability among lakes, we used SDF and littoral area as physical descriptors and alkalinity (ppm), specific conductivity (μS/cm), and pH as chemical descriptors. We expected that conductivity would be related to electrofishing efficiency (Reynolds 1996) but that alkalinity and pH could be also because all three variables tend to covary in lakes. Thus, we evaluated conductivity, alkalinity, and pH with the expectation that a correlation between catch rate and any of these three variables would indicate an underlying effect of conductivity. Lake variables were obtained from the Wisconsin Surface Water Inventory database (Wisconsin Conservation Department 1961–1966; Wisconsin Department of Natural Resources 1967–1983). The X variables were measured only once for each lake, so we used averages of electrofishing CPE and age-0 walleye density for lakes with estimates in multiple years ($N = 18$ lakes). To explain the variability in catchability within lakes (among years), we used the X variable temperature, which was measured at the time of sampling in a subset of lakes for which surveys were conducted in multiple years (Big Crooked, Escanaba, Lost Canoe, Plum, and Wolf lakes; Table 2). Before testing for temperature effects, we used analysis of covariance (ANCOVA) to test for homogeneity of slopes (lake × density interaction) and intercepts (lake main effect) among lakes. The parameters for the among-lake and within-lake models were estimated from the $\log_e$ transformed equation using ordinary least squares (multiple linear regression), that is,

$$\log_e\left(\frac{C}{f}\right) = b_0 + b_1 \log_e\left(\frac{N}{A}\right) + b_2 \log_e X_1 + \cdots + b_n \log_e X_n,$$ (6)

We tested each X variable individually as an added variable in the relationship between and judged a variable to be important if the estimated coefficient was significantly larger than its standard error ($P \leq 0.05$).
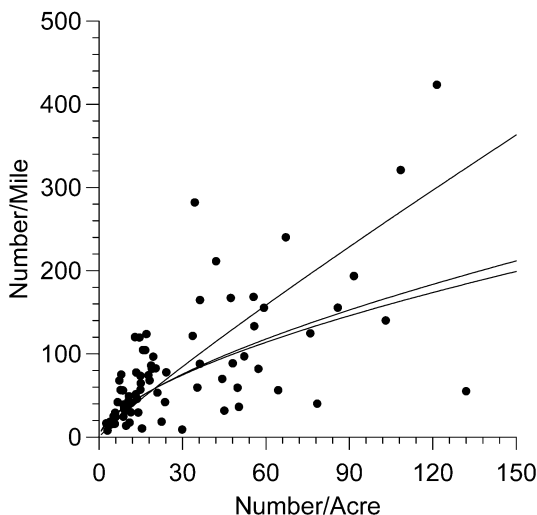
FIGURE 2.—Electrofishing catch rate (number/mi) as a function of age-0 walleye population density (number/acre) in 19 northern Wisconsin lakes during 1958–1999. The lower curve is the ordinary-least-squares regression line, the middle curve the bias-corrected line, and the upper curve the geometric mean functional regression line; solid circles indicate observed values.
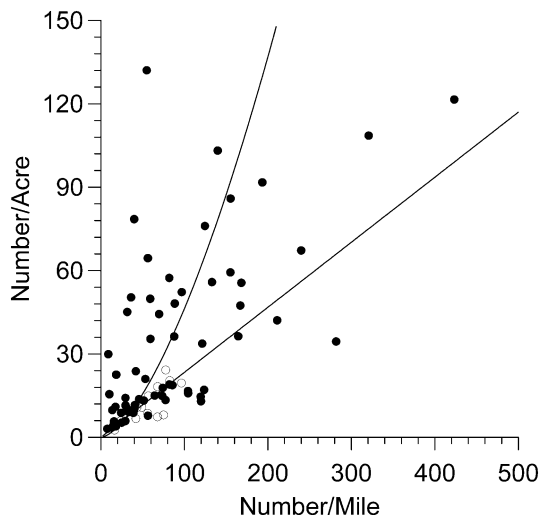

FIGURE 3.—Age-0 walleye population density (number/acre) as a function of electrofishing catch rate (number/mi) in 19 northern Wisconsin lakes during 1958–1999. The lower curve represents Serns' (1982) linear model, which was based on the data shown as open circles; the upper curve represents the bias-corrected model from the present study, which was based on all of the data points shown (both solid and open circles).

Results

Between 1958 and 1999, the abundance of age-0 walleyes was estimated 94 times in 27 lakes; 21 of these estimates from 13 lakes were included in Serns' (1982) analysis. We excluded 17 estimates from 14 lakes because the coefficient of variation was larger than 0.40 or because the standard deviation of the estimate could not be determined; 8 of the excluded estimates from 8 lakes were from Serns' (1982) analysis (Table 2). We therefore included 77 estimates from 19 lakes in our analysis, of which 64 estimates from 14 lakes were newly collected for this study (Table 2). Age-0 walleye abundance was estimated in more than one year in Escanaba Lake (39 years), Big Crooked Lake (6), Wolf Lake (6), Sparkling Lake (4), Plum Lake (3), Lost Canoe Lake (3), Bearskin Lake (2), Big St. Germain Lake (2), and Butternut Lake (2). Age-0 walleye abundance was estimated in only one year in 10 lakes.

Electrofishing catch rate was nonlinearly related to the population density of age-0 walleyes in northern Wisconsin lakes, and the bias-corrected relationship was closer to the ordinary-least-squares regression than to the GM functional regression. The bias-corrected slope of the relationship between $\log_e$ transformed CPE and $\log_e$ transformed density was significantly less than 1.0

(simulated 95% CI = 0.602–0.709), indicating that the relationship between electrofishing CPE and density was nonlinear (Figure 2):

$$\frac{C}{f} = 8.601\left(\frac{N}{A}\right)^{0.639}. \qquad (7)$$

The bias-corrected relationship between electrofishing catch rate and age-0 walleye population density was much closer to the ordinary-least-squares regression ($\alpha = 9.415$; $\beta + 1 = 0.609$) than to the GM functional regression ($\alpha = 3.901$; $\beta + 1 = 0.905$).

The ratio of measurement errors between electrofishing catch rate and age-0 walleye population density was 9.032, which suggests that the ratio of measurement errors between density and electrofishing catch rate was 0.111. Consequently, the bias-corrected slope of the relationship between $\log_e$ transformed density and the $\log_e$ transformed catch rate was significantly greater than 1.0 (simulated 95% CI = 1.527–1.634; Figure 3):

$$\frac{N}{A} = 0.0345\left(\frac{C}{f}\right)^{1.564}. \qquad (8)$$

The bias-corrected relationship between age-0 walleye population density and electrofishing catch rate was substantially different from the model esti-
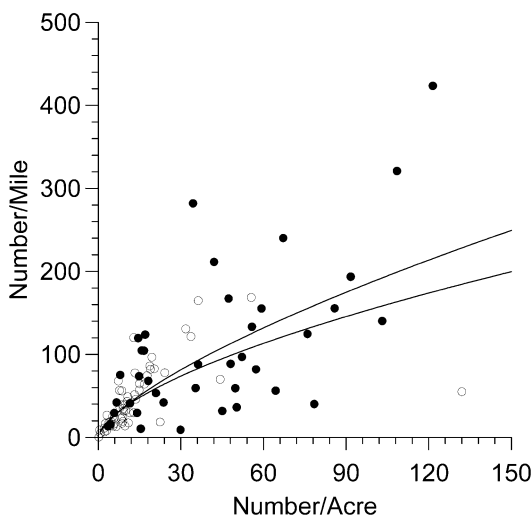
FIGURE 4.—Electrofishing catch rate (number/mi) as a function of age-0 walleye population density (number/acre) in Escanaba Lake ($N = 39$; solid circles and lower curve) and in 18 other northern Wisconsin lakes ($N = 38$; open circles and upper curve) during 1958–1999.

mated by Serns (1982), who fit an ordinary-least-squares regression through the origin; that regression had a constant slope ($\alpha = 0.234$) and no departure from linearity ($\beta + 1 = 1.0$).

The catchability of age-0 walleyes to electrofishing was similar between Escanaba Lake and the other lakes and declined with increasing population density (Figure 4). The degree of curvature in the relationship was similar between Escanaba Lake and the other lakes; the slopes of the linear relationships between $\log_e$ transformed CPE and $\log_e$ transformed density did not differ significantly (ANCOVA interaction: $F_{1,73} = 0.043$, $P = 0.837$). In addition, the intercepts of the linear relationships between $\log_e$ transformed CPE and $\log_e$ transformed density did not differ significantly between Escanaba Lake and the other lakes (ANCOVA main effect: $F_{1,73} = 0.020$, $P = 0.889$).

The catchability of age-0 walleyes to electrofishing was positively related to the variation in specific conductivity among northern Wisconsin lakes, but other physical and chemical variables failed to describe significant residual variation in the relationship between the $\log_e$ transformed catch rate and $\log_e$ transformed density. The model containing the average transformed values of CPE and density for each lake was similar to the model that included all annual values for all lakes surveyed and explained 40% of the variation in electrofishing catch rate ($F_{1,17} = 10.9$, $P = 0.004$):

$$\frac{C}{f} = 8.926\left(\frac{N}{A}\right)^{0.643}. \tag{9}$$

Specific conductivity explained significant residual variation in the relationship between $\log_e$ transformed CPE and $\log_e$ transformed density ($t = 1.810$, df $= 16$, $P = 0.089$). The model that included specific conductivity explained 49% of the variation in the electrofishing catch rate of age-0 walleyes ($F_{2,16} = 7.8$, $P = 0.004$) and indicated that the electrofishing catch rate was positively related to specific conductivity within the range observed at the time of sampling (Figure 5):

$$\frac{C}{f} = 1.549\left(\frac{N}{A}\right)^{0.699} \cdot \text{Conductivity}^{0.373}. \tag{10}$$

Shoreline development factor ($t = 0.815$, df $= 16$, $P = 0.427$), littoral area ($t = -0.044$, df $= 16$, $P = 0.862$), alkalinity ($t = 1.780$, df $= 16$, $P = 0.094$), and pH ($t = 0.564$, df $= 16$, $P = 0.581$) each failed to describe significant additional variation in the relationship between $\log_e$ transformed CPE and $\log_e$ transformed density.

The catchability of age-0 walleyes to electrofishing was significantly related to the variation in temperature at the time of sampling. because temperature described significant residual variation in the relationship between $\log_e$ transformed CPE and $\log_e$ transformed density. The relationships between electrofishing catch rate and age-0 walleye density did not differ significantly among lakes (lake × density interaction: $F_{4,47} = 0.59$, $P = 0.67$; lake main effect: $F_{4,47} = 0.24$, $P = 0.92$). The model for the subset of lakes with CPE and density estimates in multiple years was similar to the model that included all lakes surveyed in all years and explained 43% of the variation in the electrofishing catch rate ($F_{1,55} = 41.6$, $P \leq 0.001$):

$$\frac{C}{f} = 8.045\left(\frac{N}{A}\right)^{0.637}. \tag{11}$$

Temperature explained significant residual variation in the relationship between $\log_e$ transformed CPE and $\log_e$ transformed density ($t = -2.032$, df $= 54$, $P = 0.047$). The model that included temperature explained 47% of the variation in the electrofishing catch rate ($F_{2,54} = 24.0$, $P \leq 0.001$) and indicated that the electrofishing catch rate was negatively related to temperature over the range of temperatures observed in Wisconsin lakes (49–71°F; Figure 6):

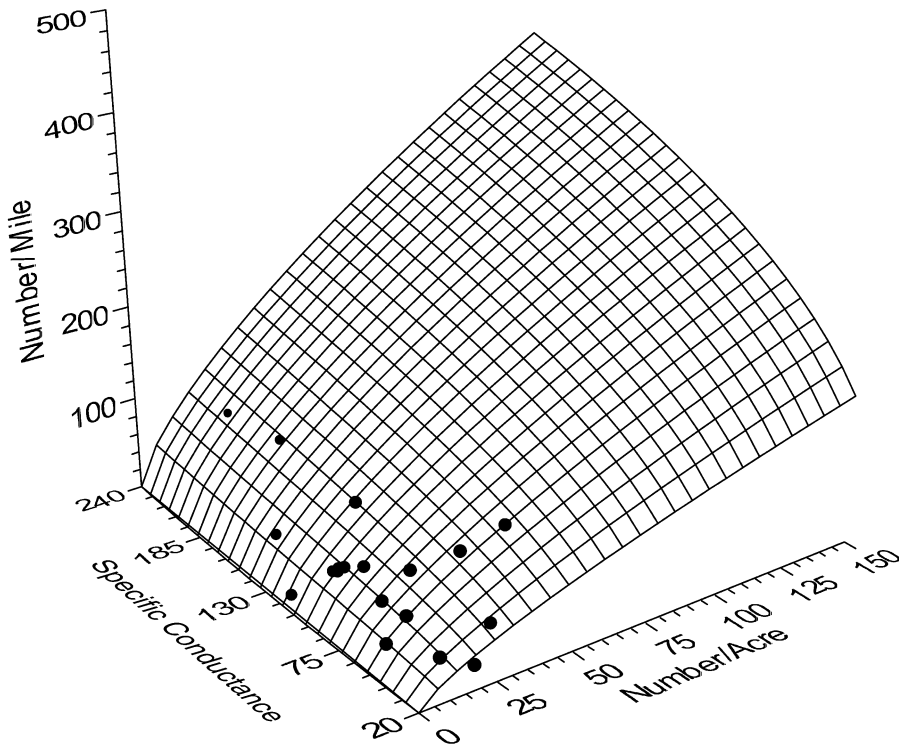$$\frac{C}{f} = 31{,}101\left(\frac{N}{A}\right)^{0.686} \cdot \text{Temperature}^{-2.045}. \tag{12}$$

FIGURE 5.—Electrofishing catch rate (number/mi) as a function of age-0 walleye population density (number/acre) and specific conductivity (μS/cm) in 18 northern Wisconsin lakes during 1958–1999. The response surface shows the statistical relationship and the solid circles the observed values.

Discussion

We found that the catchability of age-0 walleyes to electrofishing was negatively related to age-0 walleye population density in Wisconsin lakes, as has been shown for other species and capture methods (Peterman and Steer 1981; Arreguin-Sanchez 1996; Shuter et al. 1998; McInerny and Cross 2000). Catchability varies inversely with fish population density whenever nonrandom methods are used to harvest aggregations of fish, as in the case of active-capture fisheries pursuing schools of fish (Peterman and Steer 1981; Arreguin-Sanchez 1996). Similarly, catchability may vary inversely with density whenever the fishing gear becomes saturated, such as when dense aggregations are fished (McInerny and Cross 2000). For example, the electrofishing catchability of largemouth bass *Micropterus salmoides* longer than 200 mm varied inversely with population density in Minnesota lakes, probably because dipnetting efficiency declined as density increased (McInerny and Cross 2000). Similarly, the densities of age-0 walleyes in our study were sometimes great enough to cause dipnetting efficiency to decline due to handling time

constraints. The range of densities analyzed by Serns (1982) was much narrower than the range we analyzed (even if we had excluded data for Escanaba Lake; Figures 2, 4), so we were more likely to detect the density dependence of catchability. Reanalysis of Serns' original (1982) data with our model indicated no evidence of density-dependent catchability ($b_1 = 0.921$, 95% CI = 0.706–1.136) with a slope near the origin ($b_0 = 0.285$, 95% CI = 0.129–0.629) that is similar to the slope estimated by Serns (1982).

Our estimates of age-0 walleye population density relied on a single capture method for marking and recapturing fish and on fin removal as the marking method, which could bias the estimates through gear avoidance or unequal capture probabilities of marked and unmarked walleyes. We used the same capture method for marking and recapturing age-0 walleyes because age-0 and age-1 walleyes aggregate inshore at night during fall and so are fully vulnerable to capture by nighttime electrofishing (Serns 1982, 1983). We sampled entire lake shorelines to ensure that marked and unmarked fish were equally vulnerable to sampling
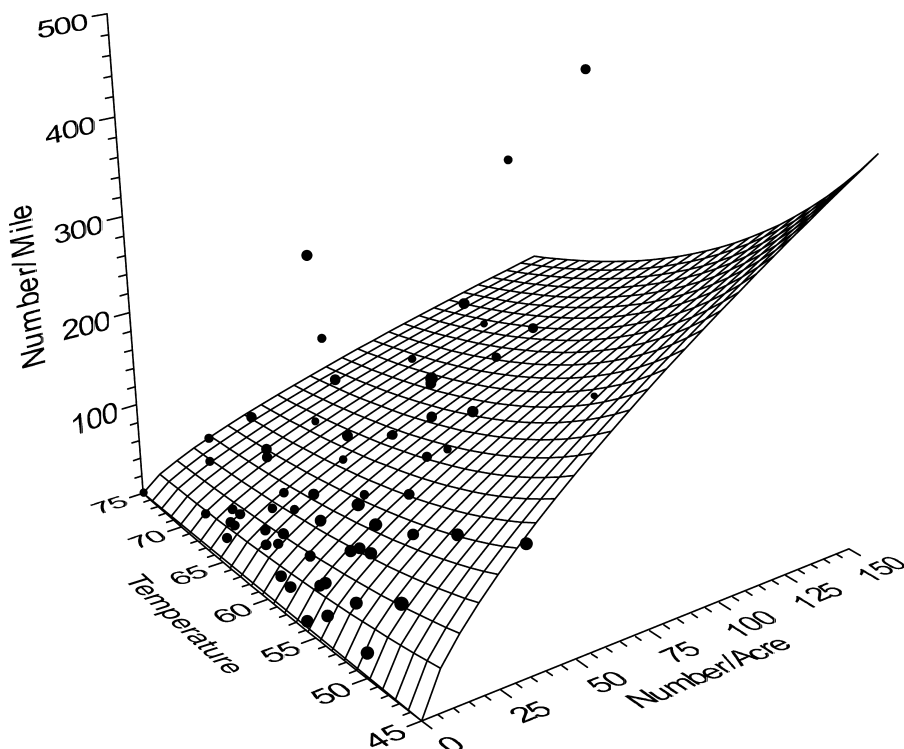
FIGURE 6.—Electrofishing catch rate (number/mi) as a function of age-0 walleye population density (number/acre) and temperature (°F) in five northern Wisconsin lakes (Big Crooked, Escanaba, Lost Canoe, Plum, and Wolf lakes) during 1958–1999. The response surface shows the statistical relationship and the solid circles observed values.

because the interval between marking and recapturing was too short to permit marked and unmarked fish to fully mix. We used fin removal to mark fish because it does not affect the survival or vulnerability to capture of age-0 walleyes (Churchill 1963).

We found that the parameters of the relationships between catch rate and fish population density were more accurately estimated by ordinary-least-squares regression than by GM functional regression because the measurement errors in the electrofishing catch rate were more than nine times as great as those of age-0 walleye density. Ricker (1975) suggested that GM functional regression should be used whenever the independent variable is estimated with substantial error. Based on Ricker's (1975) recommendation, tests of density dependence of catchability have often relied on GM functional regression as a way of accounting for measurement errors in fish density (Peterman and Steer 1981; Hansen et al. 2000; Newby et al. 2000). However, GM functional regression assumes that measurement errors are the same in the dependent and independent variables and therefore

overestimates the slope of any relationship for which measurement errors are greater in the independent variable than in the dependent variable (as we found in the present analysis).

We found that the variation in specific conductivity among lakes explained significant residual variation in the relationship between electrofishing CPE and age-0 walleye population density but that the variation in other physical and chemical features among lakes did not significantly affect catchability. Electrofishing catch rates vary spatially in response to many factors, such as presence of the species in the littoral area, water clarity, water conductivity, cover, and bottom substrate (Reynolds 1996). Conductivity is a measure of the ability of water to carry electrical current, so is the most important environmental measurement related to electrofishing (Reynolds 1996). The effect of conductivity on electrofishing catchability depends on whether fish conductivity is greater than, less than, or equal to water conductivity. In low-conductivity lakes like those in our study, conductivity should be directly related to fish response (and hence catchability) for any given volt-

age potential because the applied power approaches the response threshold as conductivity increases (Reynolds 1996). For this reason, we found that electrofishing CPE was directly related to conductivity. In high-conductivity lakes, such as those studied by Hill and Willis (1994), conductivity should be inversely related to fish response for any given voltage potential because the applied power moves further from the response threshold as conductivity increases (Reynolds 1996). For this reason, Hill and Willis (1994) found that the electrofishing catch rate of largemouth bass was inversely related to conductivity. In intermediate-conductivity lakes, such as those studied by McInerny and Cross (2000), conductivity may be unrelated or inconsistently related to fish response because the applied power is close to the response threshold (Reynolds 1996). For this reason, McInerny and Cross (2000) may have found that the electrofishing catch rate of largemouth bass was unrelated to conductivity during daytime in fall and nighttime in spring, inversely related to conductivity during nighttime in fall, and directly related to conductivity during daytime in spring.

We found that the variation in temperature within lakes explained significant residual variation in the relationship between electrofishing CPE and age-0 walleye population density, which generally agrees with the results of Borkholder and Parsons (2001). Water temperature affects electrofishing efficiency indirectly (by altering fish distribution in relation to effort) and directly (by altering fish metabolism and water conductivity; Reynolds 1996). For example, Borkholder and Parsons (2001) found that the electrofishing catch rate of age-0 walleyes in Minnesota lakes increased as temperature cooled from 75°F to 66°F and then decreased as temperature cooled further to 39°F. In our study, the observed negative effect of temperature on the electrofishing catch rate of age-0 walleyes in Wisconsin lakes may have been due to the fact that the range of temperatures we tested (49–71°F) was narrower and toward the lower end of the range tested by Borkholder and Parsons (2001).

We found a large residual variability in the relationship between electrofishing catch rate and age-0 walleye population density even after accounting for the variability associated with conductivity and temperature. The potential causes of such large residual variability include variation in biological factors such as fish size; environmental factors such as water transparency, dissolved oxygen concentration, substrate, rain, and wind; and technical factors such as power output, crew ex-

perience, boat and electrode configurations, crew size, and boat speed (Reynolds 1996). The effect of fish size was probably not great because we sampled only age-0 walleyes, which occupy a relatively narrow size range. We could not address several potentially important environmental factors such as water transparency, dissolved oxygen concentration, rain, or wind because such variables are not temporally stable and were not collected at the time of sampling. In further studies, we plan to add measurement of these factors to the standard operating procedures for electrofishing surveys, so that their importance can be evaluated. The effects of technical factors were controlled as much as possible during our study to minimize their individual effects. For example, boat operators were responsible for adjusting power output to achieve uniform taxis and narcosis, experienced crews conducted all surveys, boats and electrode configurations were of standard design and construction, crew sizes varied only in terms of the number of additional members available to process fish while running, boats were operated at consistent speeds around the shoreline, and sampling was never stopped or reversed.

Our results showed that the electrofishing catch rate was not linearly related to the population density of age-0 walleyes in northern Wisconsin lakes, whereas Serns (1982) assumed that the relationship was linear. In part, our model differed greatly from Serns' (1982) model because the measurement errors in electrofishing CPE (Serns' independent variable) greatly exceeded the measurement errors in age-0 population density (Serns' dependent variable). Our model demonstrated that electrofishing CPE became increasingly less useful as a predictor of age-0 walleye population density as population density increased. In addition, our analysis illustrated how measurement errors, which are often ignored, can influence tests of important relationships in fisheries data. Despite its crudeness as a predictor of population density, the electrofishing catch rate of age-0 walleyes is a fast and efficient method for obtaining information on relative year-class strength. However, we recommend that electrofishing catch rate only be used as a crude index, rather than a predictor, of age-0 walleye population density. For example, an electrofishing catch rate that suggests a density of 10–30 age-0 walleyes per acre provides information that is very useful to a fishery manager because it indicates that a strong year-class is present, that stocking is unnecessary, or that the habitat is adequate to support a self-sustaining population.

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